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LYSOROPHUS, A PERMIAN URODELE.

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Thirty-one years ago Professor Cope described¹ briefly three small and incomplete vertebræ from the "Permian" of Vermilion County, Illinois, as those of a reptile under the name *Lysorophus tricarinatus*. The type specimen was figured, with additional descriptions, by Case in 1899.² In a later paper³ Case recognized the same form from the Permian of Texas and gave a good description and figures of the vertebræ and ribs. From the peculiar coiled condition of the various intermingled series of vertebræ which he had himself collected he concluded that the animal was long and snake-like. No limb or pectoral or pelvic bones have ever been detected. Associated with the form but not definitely connected with the vertebræ was a fragment of the skull of a small animal which he doubtfully referred to the same species, but which he also was inclined to refer to *Isodectes* Cope. In 1904 Broili⁴ with real skull material and less perfect vertebræ, reached the startling conclusion that the genus showed certain affinities to the fishes, because of the presence of what he thought were gular plates in the palatine region. Chiefly because of their supposed presence he proposed the family name Paterosauridæ for the genus, which he located in the Rhynchocephalia. It is needless to say that his views of the diphylectic origin of reptiles, one phylum directly from the fishes, the others from the amphibians, has been received by naturalists with doubt and incredulity, and are, as will be seen, wholly unsubstantiated by this animal. His "gular plates" were doubtless merely misplaced proatlas bones. It is rather surprising that he should have overlooked the almost impossible reptilian char-

¹ *Proc. Amer. Phil. Soc.*, 1877, p. 187.

² *Journal of Geology*, V., p. 714, pl. II., ff. 12a, 12b, 12c.

³ *Ibid.*, May, 1892, p. 46, pl. IX., ff. 1, 2.

⁴ *Paleontographica*, LI.

acters of the vertebræ and skull, characters certainly impossible for a rhynchocephalian.

Recently, in examining the material in the Chicago collections, the remarkable characters of the vertebræ, so anomalous for any reptile, and utterly unknown in this class from the Permian otherwise, aroused my interest and doubt. From the matrix containing several series of vertebræ a corner of a bone protruded which I recognized as of a mandible. Under the skillful manipulations of Mr. Paul Miller a wonderfully complete and undistorted skull was brought to light. In similar matrix, and associated with vertebræ of the same kind I recognized another mandible and several small, pitted dermal bones, probably belonging to another type of amphibian, though it is not impossible the scutes were those of *Lysorophus*.

That the present species belongs in the genus *Lysorophus* from the reputed Permian of Illinois seems tolerably well assured, though the type material of the genus is rather scanty, and not entirely sufficient to resolve doubt. That the species are identical is I believe quite improbable. With this understanding, however, it will do no harm to use Cope's name for both genus and species until such time as more and better material of the species has been obtained from the original or contemporaneous beds.

LYSOROPHUS TRICARINATUS Cope.

Skull (Figs. 1-3).—The general shape of the skull is that of a four-sided pyramid, pointed anteriorly. The upper surface is nearly plane, very gently convex from side to side, and also longitudinally in front. The sutures are widely separated in the specimen, indicating a loosely joined skull, and the bones are quite smooth, without pittings or mucous canals. The nasals are relatively large bones, with nearly parallel sides, rounded anteriorly. The frontals are also four-sided, the longer sides nearly parallel; the bone is about twice as long as wide. On either side, beginning at the transversely extended fronto-parietal suture, there is a narrow bone which seems to be continuous as a single element to beyond the middle of the nasals, ending acuminately in front. This is doubtless the prefrontal of the modern urodeles. The parietals are broad and large bones, like

the frontals with nearly parallel sides, overhanging, for the most part, the open temporal region. There is no parietal foramen. They are gently convex from side to side. From this posterior suture the upper surface of the skull turns downward at an angle of about twenty degrees, so as to bring it nearly parallel with the plane of the lower margins of the mandibles. Three rather large bones are seen here, a median unpaired one and two larger lateral ones. The median bone is broader in front than behind and borders the large foramen magnum; it doubtless corresponds to the median cartilage found in many urodeles, called the supra-occipital usually, by Gaupp the tectum synoticum. The lateral

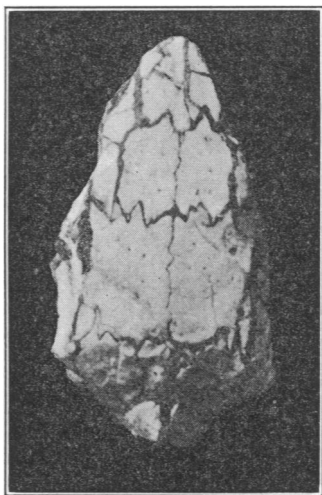


FIG. 1. *Lysorophus tricarinatus*, skull from above, enlarged three diameters.

bones are larger, of an irregularly square shape with a hook-like prolongation exteriorly behind, turned downward back of the squamosal. They must be identified as "epiotics," a bone rarely if ever found separate in the modern batrachians. The squamosal (paraquadrate of Gaupp) unites, by a nearly straight antero-posterior suture, with the parietal and epiotic and then turns downward, forward and a little outward, narrowed and more rod-like below. There is some doubt of its union with the quadrate, but the division seems apparent on each side. With this interpretation, the quadrates are small bones, about twice as

long as wide terminating in the cotylus, and perforated a little above the lower extremity by a foramen. The double occipital condyles are sessile, each with an oblique, flattened articular face looking inward and backward. Just in front of the condyles exteriorly there is a small foramen for the vagus, in front of which there is a large vacuity for the ear opening, partially or imperfectly closed in front by this combined bone. Above, the bone sends a triangular prolongation inward to the lower edge of the supraoccipital, bordering the hind margin of the epiotic. The large foramen magnum is thus bordered as in modern urodeles, nearly completely, by the exoccipital. Rather closely applied to this margin is a pair of triangular bones meeting roof-like in the middle above and terminating below in an angle a little above the condyles. They occupy the position of, and doubtless are the so-called proatlas bones, displaced to form the "gular plates" of Broili. The basioccipital bone I at first thought to be ossified, but further examination convinces me that the broken surface seen in the specimen between the condyles below is the broken off anterior end of the atlas. A like condition was found by Broili in his specimens, but he interpreted the structure as that of a broken off occipital condyle. Furthermore, a little in front of this fractured surface is seen the hind margin of a thin transverse plate, the parasphenoids.

In the palatal region are lying four pairs of branchial bones, with no indications whatever of so-called gular plates. The position and relations of these bones are well shown in the accompanying photograph (Fig. 3). The outer pair lying close to the inner margins of the mandibles, have the posterior end thickened and recurved, hook-like, to abut against or approach the hind side of the quadrate. I would take them to be ceratobranchials save for the fact that a pair of nearly square bones very clearly articulate with the anterior ends, which must be ceratobranchials. To the inner side, and progressively more posterior, lying symmetrically, are three pairs of epibranchials the inner and hindmost represented in the specimen only by their anterior ends, the posterior portions broken off with the atlas. The two outer pairs, at least, are thickened and truncate at each end, and are partly hollowed or cancellated, like all other bones of the skeleton. The first of

these pairs also seems to have a thickened and recurved posterior extremity. The mandibles are rather stout, extending a short distance back of the cotylus, expanded and flattened, somewhat spout-like in front. Each bears about twelve, conical, simple teeth on the anterior, somewhat concave margin, which is about two

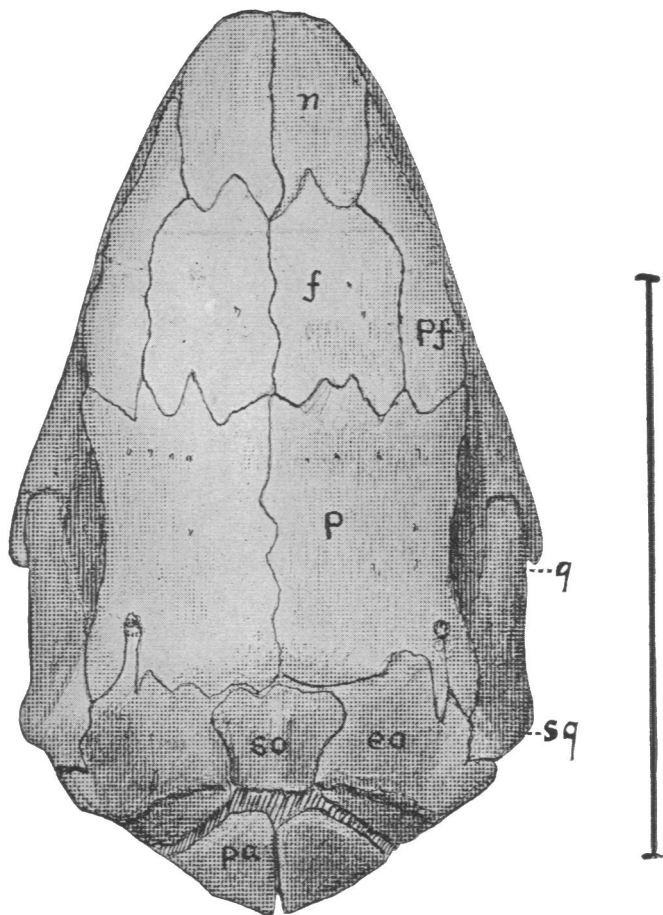


FIG. 2. *Lysorophus tricarinatus*, skull from above, enlarged five diameters. *n*, nasal; *f*, frontal; *pf*, prefrontal; *p*, parietal; *so*, supraoccipital; *eo*, epiotic; *pa*, proatlas.

fifths the length of the mandible; the teeth are directed somewhat obliquely outward.

The sides of the skull are in a nearly vertical plane, directed

somewhat obliquely outward posteriorly. The squamosal and quadrate, extending downward, forward and a little outward, meet the cotylus of the mandible a little back of the middle of the skull. Opposite the mandibular teeth in front are the narrow maxillæ, with teeth like those of the mandibles. They end freely and acuminate behind, and if connected at all with the bones of the upper part of the skull, the connection was small and slender and situated far forward. The whole side of the skull, from in front of the squamosal and quadrate seems to have been unossified; there are no jugals nor quadratojugals, and no temporal arches. The premaxillæ are also very slender, with four or five small teeth on each side. The position of the eyes was far forward, in the narrow space between the maxillæ and the prefrontals, and it is quite certain that these organs must have been very small. The nares also must have been minute and situated far forward, probably between the nasals and the premaxillæ near the middle line. Altogether, in life, save for its greater narrowness and more snake-like appearance the whole head must have been strikingly like that of *Necturus*.

Vertebrae.—The centrum is moderately elongated, deeply biconcave with persistent notochord, wholly without trace of hypocentra. In the middle below there is a median rounded keel, concave longitudinally, with a deep pit or fossa on each side reaching nearly to the internal cavity. On either side there is another, more slender carina, bounding the fossa above, with a more shallow concavity above it. The pedicel is elongate antero-posteriorly, the neural canal large. The centrum has no parapophysial facet or process for the rib. A little below and back of the anterior zygapophyses is the diapophysis, a flattened process directed anteriorly and a little downward, with the extremity thickened and a little rounded; they are short. The arches are depressed, a little convex in the middle anteroposteriorly, but without spine, the two sides separated by a persistent median suture, and the two bones are usually drawn somewhat apart, like the bones of the skull. The zygapophyses are rather large, flattened on their articular surface and are directed somewhat inwards or outwards. The ribs are large, flattened proximally, more cylindrical distally and are hollow. They have an

anterior angulation or curvature near the proximal third, this third being directed more obliquely backward. There are no traces of abdominal ribs in the numerous specimens examined, nor any of dermal plates, save in the case already spoken of, plates evidently belonging with a small mandible near them of an apparently different type from that of *Lysorophus*.

The terminal part of the tail, which is preserved in one speci-

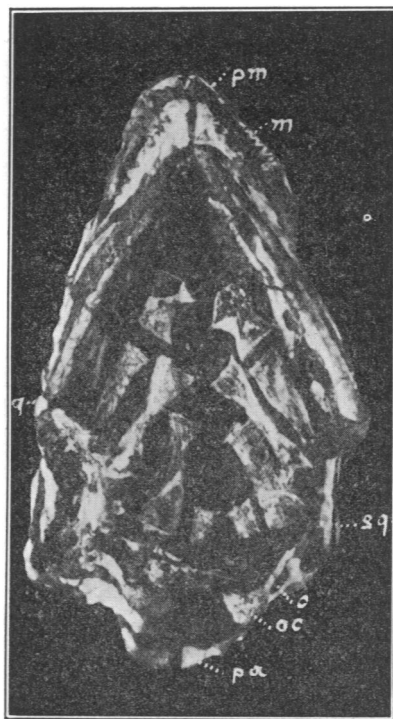


FIG. 3. *Lysorophus tricarinatus*, skull from below, enlarged five diameters. *pm*, premaxilla; *m*, maxilla; *sq*, squamosal; *o*, otic fenestra; *oc*, occipital condyle; *pa*, proatlas.

men, ends rather gradually, tapering to a point. In the seventeen vertebræ of the series there are no ribs and no diapophyses, or very rudimentary ones anteriorly; and I can find no traces of chevrons. Characteristic figures of the vertebræ and ribs will be found in the cited papers of Case.

That *Lysorophus* is not a reptile requires no argument—the

unpaired supraoccipital, the absence of pineal foramen, quadra-tojugals, jugals, postfrontals, temporal arches, the evidently large parasphenoid, the double occipital condyles, paired branchials, neurocentral, single-headed ribs, etc., are positive evidence that the animal is not only not a reptile but that it is related to the modern urodele amphibians. In skull structure the characters are urodelan in every detail save the separated "epiotics," the intercalary of Cuvier, Vrolik and Cope, the paroccipital plates of Baur, the posttemporals of Broom; and this separation is precisely what would be expected in the early urodele. The exoccipitals otherwise seem to be a single bone in *Lysorophus*, but it is very probable that they are the result of an early fusion of the exoccipitals, paroccipitals and prootics. The squamosals and quadrates have the position and relations of modern salamanders, the quadrate rather better ossified than is usually the case. That the supraoccipital should be ossified is, also, what might be expected. The remarkable fact that this bone should be unpaired while all the remainder of the bones of the skull are very loosely joined, as also the fact that the corresponding element in the urodeles is cartilaginous would seem to preclude its identification with the paired supraoccipital plates, the postparietals of Broom, of the Stegocephalia, rather favoring Gaup's contention of the nature of his *tectum synoticum*.

The tricarinate structure of the vertebral centra is quite aberrant for a reptile, but not remarkable for a urodele; so also is the sutural division of the neurocentra, and, for the Permian, the neurocentral attachment of the single-headed ribs. The only aberrant character to distinguish *Lysorophus* from the Urodela is the long and rather broad ribs, unknown among these modern animals or their possible ancestors the Branchiosauria. It is, however, very evident that the earliest ancestors of both these groups must have long ribs, and their persistence in *Lysorophus* would be nothing remarkable. Nor do I think it impossible that *Lysorophus* and its immediate kin may have developed long ribs from the earlier short ones. Certain it is that this character alone, and it is the only aberrant one, should not exclude *Lysorophus* from the Urodela, though it may necessitate a slight revision in the definition of the group. That *Lysorophus* cannot

be classed with any of the divisions of the so-called Stegocephalia is quite as evident as its exclusion from the Reptilia; and upon the ribs alone the formation of a new order of Amphibia would not be at all justified.

That the genus represents a distinct family of the Urodela is of course obvious. Broili, under the erroneous supposition that it is a reptile of the order Rhynchocephalia gave to it the name Paterosauridæ, to indicate its "paternal" relationship with the reptiles. But this name was chosen in direct contravention of the rules of zoological nomenclature, since it is not represented by a genus in the group, and since any one is at entire liberty to apply the stem as a generic name in another group. The name is not tenable, and should be replaced by Lysorophidæ.

The condition in which the remains of so many of these animals are found, numerous series intermingled in vertical and lateral curves, is I think conclusive evidence that death overtook the creatures in the drying up of ponds and pools of water. That the animals were snake-like in life is of course proven by the long connected series of vertebræ of nearly uniform size. That they had but feeble power of sight is also assured by the very small size of the eyes. That they were perenni-branchiate is I believe also extremely probable from the large size of the branchiæ, and the manner in which these creatures represented by their known remains met their death. Doubtless also they were bare skinned and more or less mud burrowing in habit. That *Lysophorus* stood in direct ancestral relationship to such forms as *Necturus* or *Proteus* is rather improbable, but that it was very close of kin to the ancestors of these forms I do believe to be very probable.

SALAMANDER-LIKE FOOTPRINTS FROM THE TEXAS RED BEDS. (Fig. 4.)

Recently, Miss Augusta Hasslock, of the Abilene, Texas, High School, has had the kindness to send me a number of thin red shales showing abundant markings of raindrops, worm or other tracks and footprints which must have been made by some salamander-like creatures of small size. The horizon is assumed to be Permian, but the fact that the shales occur not far below the

Cretaceous, inclines me to the belief that it will eventually be found to be Triassic. Enlarged photographs are given of some of the best of these numerous prints. The reverse of those at *a* and *b* are shown in *a*¹ and *b*¹. In the lower, left corner is shown the figure of a much larger print. It will be observed that the prints occur in pairs, one with clear evidence of five, the other with but four toes, from which the conclusion is justified that the crea-



FIG. 4. Footprints from the red beds of Texas, near Abilene, enlarged about one third.

tures were tetradactyl in front, pentadactyl behind, as were the Branchiosauria and as are the Urodela of to-day. Whether or not they were real salamanders which made the prints, or branchiosaurs, cannot be determined, but I am inclined to believe, in the light of the evidence presented by *Lysorophus*, that the origin of

some or all of these prints is due to real salamanders of modern type.

VENTRAL RIBS IN *LABIDOSAURUS INCISIVUS*. (Fig. 5.)

In a recent paper¹ I stated my belief that ventral ribs would eventually be found in some of the forms now classed in the rather heterogenous group known as the Cotylosauria, and I suspected that the specimen of *Labidosaurus* therein described presented such evidence, but could not be sure. This evidence has, however, been made clear by further preparation of that specimen. In the removal of the matrix from the under side of the pubes a small fenestra of accidental origin was found, and in this

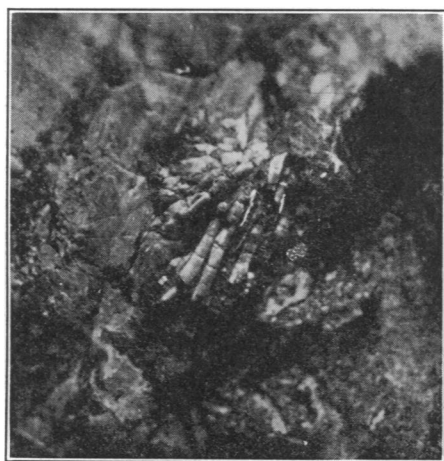


FIG. 5. Ventral ribs of *Labidosaurus incisivus*, enlarged about two diameters.

space, that is originally between the front end of the plate-like pubes and the vertebræ, are seen abundant evidences of small slender ribs, of some of which I give herewith a photographic illustration. At this spot seven ribs are seen lying closely together and parallel, directed from the anterior outer corner of the pubis inward and backward. Still further forward, and the continuation of these series, are further evidences of the same sort. The ribs are much smaller than I had expected to find them, but it is clear to me that the whole under side of the abdomen was enclosed in a closely set armor of slender ossified ribs. This char-

¹ *Journal of Geology*, XVI., p. 148, 1908.

acter adds another evidence of the relationship between the Procolophonia and *Labidosaurus*, and destroys its value as a group distinction.

Addenda. — Texas Permian Fields, September 25. Since the manuscript of the foregoing left my hands I have seen the recent paper by Case (Bull. Amer. Mus. Nat. Hist., xxiv, 531, June 30, 1908), in which he recognizes the amphibian nature of *Lysorophus*, figuring the skull with its exposed palate. He does not, however, discuss the relationship of the form and we differ in the interpretation of some of the bones.

Within the past week Mr. Miller, my assistant, has discovered two deposits of the species herein described from which cartloads of the peculiar nodules might be had for the digging. In two other places I have found them less abundantly. In examining the selected material, I have detected a small limb, very *Necturus*-like with four metapodials and epipodials in place, the mesopodials evidently unossified. It is of course possible, but not probable, that the limb is an accidental intrusion of some other small amphibian. My conviction is that the *Lysorophidæ* should be included in the Ichthyoidea.